ACADEMIC PRESS

Biological Control 25 (2002) 22–29

Biological Control

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Biology of *Apagomerella versicolor* (Boheman) (Coleoptera: Cerambycidae) in Argentina, a candidate for biological control of cocklebur (*Xanthium* spp.)

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Received 19 April 2001; accepted 22 March 2002

Abstract

The biology of the cerambycid beetle, *Apagomerella versicolor* (Boheman), a candidate for biocontrol of cocklebur, *Xanthium strumarium* L., in the US, was studied in Argentina where it attacks *X. strumarium cavanillesii* Love and Dansereau. *A. versicolor* is univoltine and adults appear in the field in early spring. In the laboratory, the adults lived an average of 18.5 days. Each female laid an average of 38 eggs, one egg per oviposition. The incubation period for the eggs lasted 10 days at 25 °C and 80% RH. The larval stage had seven instars. Eggs were laid in the stems and larvae fed boring their way toward the root. At the beginning of fall, larvae girdled the stem of the mature plant near the crown, causing the dried aerial part of the plant to fall over. The last instar entered diapause and pupated within the roots in dead and dry plants until spring. Exposure of larvae to temperatures lower than 12 °C for at least 8 days ended diapause. All larvae survived continuous exposure to −8 °C for 3 days, and immersion of larvae in tap water for 20 days did not affect their survival. In Buenos Aires, Argentina, three parasitoids were found attacking the larvae; a braconid, *Nealiolus* n. sp., parasitized 61.5% of the larvae in 1988. Attack by *A. versicolor* reduced fruit production in *X. s. cavanillesii* by 66%, and killed young plants. *A. versicolor* has some attributes of a biocontrol agent of *Xanthium* spp. These attributes, along with cold tolerance, immersion tolerance, broad habitat distribution from tropical forest to desert, suggest that it would be an effective biocontrol agent of *Xanthium* spp. Published by Elsevier Science (USA).

Keywords: *Apagomerella versicolor*; *Xanthium*; Cocklebur; Biological control; Weed; Cerambycidae; Asteraceae

1. Introduction

The genus *Xanthium* originated probably in South America (Ragonese and Milano, 1984) or Central and South America (Love and Dansereau, 1959). More than 30 species have been assigned to the genus (Holm et al., 1977) and various attempts have been made to classify the genus (Love and Dansereau, 1959; McMillan, 1975; Millspaugh and Sherff, 1919; Widder, 1923). The species vary greatly in size and color of the burr, the number and length of the thorns on the burrs and the degree to which the beaks (two stout hooks at the end of the bur) and the thorns are hooked (Hicks, 1971; Love and Dansereau, 1959; McMillan, 1975; Nadeau, 1961; Weaver and Lechowicz, 1983). The classification of Love and Dansereau (1959), though provisional, is widely accepted (Weaver and Lechowicz, 1983). They reduced the number of species to two: *X. strumarium* L., a highly variable species, and *X. spinosum* L., which is far more homogenous. They acknowledged two subspecies: *X. strumarium strumarium* L. and *X. strumarium cavanillesii* (Schouw) Love and Dansereau. The dispersion center of the first subspecies is the Mediterranean-Euro-Asian area and that of the second is America. *Xanthium spinosum* originated in South America (Hocking and Liddle, 1986; Ragonese and Milano, 1984).

The species of cockleburs that form the *X. strumarium* L. complex are summer annuals, which only reproduce sexually. They invade pastures, road banks, wateredges, and a broad variety of crops, and are considered among the most damaging weeds in the world

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1049-9644/02/$ - see front matter. Published by Elsevier Science (USA).
PII: S1049-9644(02)00043-9

(Holm et al., 1977). They cause losses in crop yields by competing for space, CO_2, light, and especially for water and nutrients (McWhorter and Hartwig, 1972). Charudattan and DeLoach (1988) ranked them fourth among crop weeds in the US. Cockleburs are among the major weeds affecting soybeans in the US (Barrentine, 1974; Barrentine and Oliver, 1977; Bloomberg et al., 1982; Cooley and Smith, 1973), and soybeans in some areas in Canada (Weaver and Lechowicz, 1983). Annual losses to soybeans in Arkansas and Mississippi have been estimated at over $20 million (Geddes et al., 1979). *Xanthium strumarium* is also one of the worst weeds of cotton in the US (Vargas, 1984). Cocklebur reduces animal production. The burrs stick to the manes and tails of the animals and are particularly harmful to sheep (Wapshere, 1974). In addition to this, seeds and seedlings contain carboxyatractyloside which is toxic to cattle (Cole et al., 1980) but especially to pigs (Marzocca, 1976). A lethal dose of seeds and seedlings is approximately 2% of the animal's weight (Seddon and King, 1938). This poisonous effect decreases soon after seed germination. Finally, glandular hairs on the leaves secrete a substance which produces dermatitis in persons prone to allergies (King, 1966).

In the US cocklebur is an alternate host for *Alternaria helianthi* (Schw.) which produces the alternaria leaf spot, one of the main diseases affecting sunflower crops (Quimby, 1983). Although the fungus is present in Australia, it has not been reported there on *Xanthium* (Hocking and Liddle, 1986).

Investigations have been carried out in the US, India, and Pakistan to find natural enemies for biological control of *Xanthium* spp. in Australia. The introduction of four insects produced some control or reduction in weed vigor (Julien and Griffiths, 1998). However, the rust *Puccinia xanthii* Schw. introduced accidentally from the US, produced excellent control in most of Queenland, but no control in drier areas (Julien and Griffiths, 1998).

A search for natural enemies of *X. s. cavanillesii*, the South American form of the *X. strumarium* complex, was conducted in Argentina in 1986. One candidate that arose from the screening was the stem borer *Apagomerella versicolor* (Boheman) (Coleoptera: Cerambycidae). This long-horned beetle has been described as *Saperda versicolor* Boheman, *Phytoecia sanguinicollis* Burmeister, *Apagomera suturella* Bates, *Emphytoecia versicolor* (Boheman), or *Apagomerella suturella* (Bates). Lane (1974) made the new nomenclatorial combination *A. versicolor* (Boheman) and stated that it is the sole species in the genus, and its affinities with other genera of the Aerenicini tribe are not clearly established. Despite several morphological descriptions, the biology of *A. versicolor* is almost completely unknown. The only reference on the biology of this beetle was provided by Bosq (1943) and Rosillo (1944) who mentioned *X. s. cavanillesii* as the host plant, and Gandolfo et al. (1997), who showed that *X. s. cavanillesii* plants produce fewer fruits when infested by larvae of *A. versicolor*. Our aim was to study the biology of *A. versicolor*, which is a possible candidate for biological control of cocklebur in the US.

2. Materials and methods

The research was conducted at the USDA-ARS Hurlingham facilities in the western suburbs of Buenos Aires, Argentina, between 1986 and 1989. Field studies were conducted on a large population of *X. s. cavanillesii* on the bank of the Río Reconquista, in a pasture between Hurlingham and San Miguel, 10 km from the laboratory facilities. The climatic data presented here are from 1981 to 1990, and were issued by the meteorological weather station at INTA-Castelar, 10 km south of the research site. All results are expressed as average $\pm$ SD with a few noted exceptions where the range is given.

2.1. Life cycle and seasonal occurrence

Xanthium strumarium cavanillesii is a summer annual weed, which only reproduces sexually. In Buenos Aires, seedlings are produced at the beginning of spring (September) and plants grow vegetatively throughout that season. In December (summer) the plants start to bloom, and in the fall the fruits ripen and the plants senesce (Fig. 1).

Plants and stumps of *X. s. cavanillesii* were sampled in the field from September 1987 to August 1988. To estimate the occurrence and proportion of pupae and adults, 18 samples of stumps (produced by the larvae) and dry plants (grown the previous year) were taken every 8–10 days between September 1987 and January 1988. To estimate the occurrence and density of larvae, from the first to the seventh instar, 16 samples of 100 randomly chosen plants (grown the current year) were sampled ($n = 1600$) every two weeks from October 1987 to September 1988. From October 1987 to April 1988, green plants were sampled, from April to September 1988, when green plants were not found, dry plants and stumps were sampled.

The occurrence of adults was estimated indirectly in the field by counting the adult emergence holes in the stumps and dry plants. The percentage of adults emerged in each period was determined by successive sampling. Egg occurrence was estimated by combining the results of adult fertility from the fecundity table obtained in the laboratory and the percentage of adults that emerged in the field. The proportion of larvae and pupae was obtained by direct counts. The incidence of parasitoids was obtained by counting the cocoons inside stumps and their emergence from larvae.

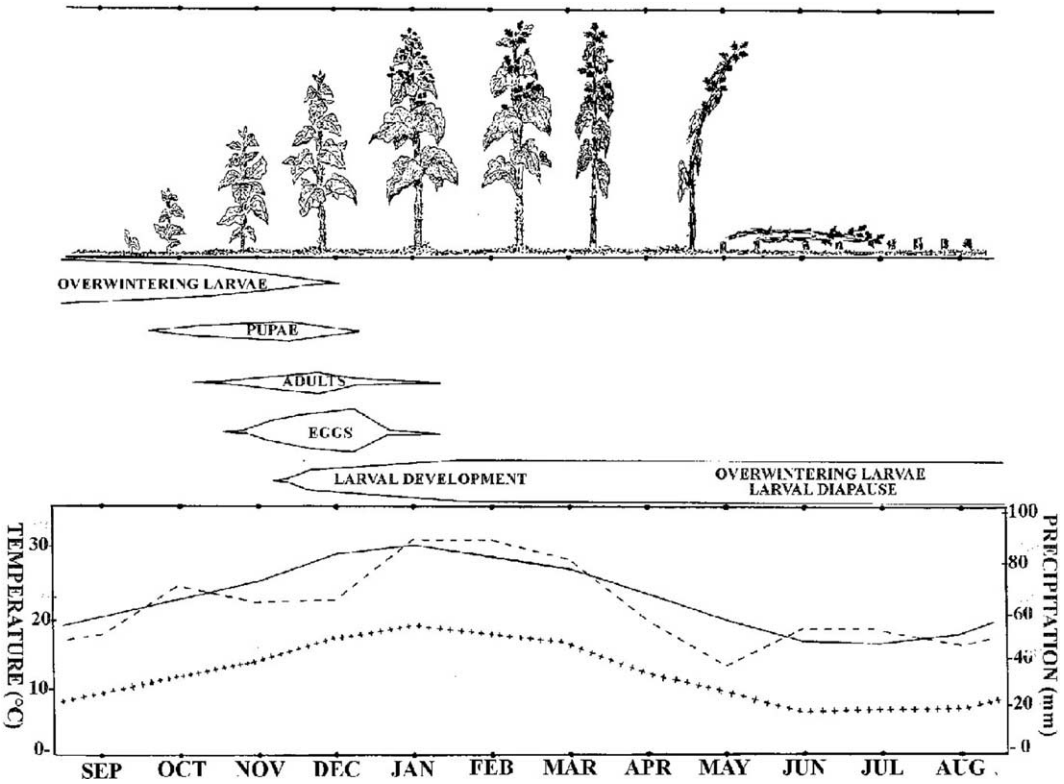

Fig. 1. Correlation of life cycle of *A. versicolor* and phenology of *Xanthium strumarium cavanillesii* with 10 year-mean monthly maximum (———) and mean monthly minimum (+++) temperatures and rainfall (----) (climate data from Estacion Castelar INTA, Buenos Aires, 1981–90).

During 1987–88 and 1988–89 the percentage of plants attacked by *A. versicolor* was estimated from 1061 and 1832 plants, respectively. About 300 plants of *X. s. cavanillesii* of different stages of development were collected in the field and dissected in the laboratory to determine the preferred oviposition sites.

The number of instars was established by measuring the width of the gula of larvae sampled in the field. In the laboratory, development of these larvae was continued in rearing chambers and the gula width was measured on exuvium and larvae after each molt. The width of the head capsule was not measured because the exuviae breaks at ecdysis. The gula also breaks, but does so in the middle and can be measured. The larval gula data were analyzed using Dyar's rule (Dyar, 1890).

2.2. Laboratory studies

Studies on fecundity, adult longevities, larval resistance to low temperature, and immersion, and calculation of the thermal constant for the pupal stage were conducted in the laboratory. We also studied the temperature required to end diapause in overwintering larvae.

The adults were collected by sweeping or with a vacuum sampler. Adults were confined in glass tubes (10 cm diameter $\times$ 25 cm high) covered with a nylon mesh, and fed with fresh leaves and stems of *X. s. cavanillesii*. The maximum number of beetles per tube was 20. Eggs and the first instar were obtained by dissecting young plants, and the last instar (seventh) was obtained by dissecting mature fruiting plants, dry stems, and stumps. Pupae were found only in roots of dry plants or stumps. No diet was accepted by the first instar. Newly emerged larvae were transferred to bits of stems of *X. s. cavanillesii* until they reached at least the fourth instar. Fourth and older instars were fed artificial diet (Harley and Willson, 1968). Last instar (seventh) and pupae were reared individually in 34-ml plastic cups with paper lids, which were filled with moist tissue paper (3/4 of total volume) to provide a humid substrate. All the insects were held at 25–30 °C, 70–80% RH, and with a 14–10 L:D photoperiod.

2.3. Reproduction and longevity

Eighteen pairs of adults that emerged from field-collected pupae were used for the study. A pair was put in a glass tube (25-cm height, 11-cm diameter) with a potted plant of *X. s. cavanillesii*. The plant was used to feed the adults and to enable the females to oviposit. The plants were changed every 3 days, and the stems were dissected to count the eggs. The ovipositional behavior was analyzed under these conditions, and under field conditions. The length, width, survival, and the incubation period at 25 °C and 80% RH were measured on 50 eggs.

2.4. Development rate of pupae

The development rate was studied to facilitate the management of the culture, and to facilitate the potential introduction of the beetles from the southern hemisphere to the northern hemisphere. Last instar (seventh) larvae were placed in rearing chambers at 15, 20, and 25 °C with 80% RH and 14–10 L:D photoperiod, and as they pupated, the development time was measured on 10 pupae at each temperature. The developmental threshold temperature and the thermal constant K were estimated by the x-intercept method using linear regression. The thermal constant K, expressed in degree-days, was calculated using the formula $K = y_i(t_i - z)$, where y_i is the average number of days to complete the pupal stage at the temperature t_i, and z is the developmental threshold temperature.

2.5. Resistance of overwintering larvae to cold and immersion

Since *X. strumarium* frequently occurs in areas likely to be flooded for several days, the ability of the insect to survive immersion was tested. Groups of 10 larvae were kept under tap water for different periods by two methods: (1) Larvae were removed from the roots and placed in small glass cylinders (15-mm diameter, 50-mm length), with nylon mesh covering both ends, and then submerged under 12 cm of water; (2) Girdled stumps containing larvae were collected undamaged and buried in a bucket of sand, leaving the stem uncovered. The bucket was then filled with water up to 12 cm above the level of the stems. In both cases, a constant temperature of 15 ± 2 °C was maintained.

The response of the insect to low temperatures was tested to determine any limitations of the species to become established in some areas of the US. Diapausing larvae were removed from the roots, individually placed in sealed glass vials, and submerged in ethanol at a constant temperature. Groups of eight larvae were held at five different temperatures (+4, 0, −4, −8, and −14 °C) for five periods (1, 3, 7, 10, and 13 days). Larvae were considered to have survived if they were alive 10 days after the experiment was finished.

2.6. Diapause

The life cycle of *A. versicolor* included a winter larval diapause. Larvae entered diapause at the beginning of autumn, and resumed their development after being exposed to low temperatures. The presence of diapause was determined by placing larvae of *A. versicolor* collected at the end of summer (they had not been exposed to temperatures below 15 °C) in a chamber at 30 °C. Less than 10% of larvae that were put in 30 °C chambers continued their development and pupated (showing no diapause), but the rest remained in the last larval instar (seventh) for at least 6 weeks. Tests were carried out in the laboratory to find the temperature required to break diapause. For this, at the end of the summer, 259 larvae were separated into 37 groups of 7 larvae each. One group was used as the control and was kept at 30 °C. The remaining groups were exposed to six temperatures (−4, 0, 4, 8, and 12 °C) for six time intervals (1, 2, 4, 8, 16, and 32 days), after which the larvae were placed in a rearing chamber at 30 °C and 80% RH.

2.7. Geographic distribution

The distribution of *A. versicolor* in Argentina was determined by collecting larvae in the field from 77 sites from 1986 to 1989. Collections in the Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires City, Museo de La Plata, Buenos Aires Province, and in the Fundación Miguel Lillo, Tucumán Province were also examined.

2.8. Parasitism

A seasonal study of the parasitoids of *A. versicolor* was conducted in the area where the life cycle was performed. Larvae and pupae were reared individually in 34-ml cups to obtain parasitoids, and examined twice a week. During 1987–88 and 1988–89, 213 and 264 larvae of *A. versicolor*, respectively, were examined for parasitoids.

3. Results and discussion

3.1. Life cycle and seasonal occurrence

Adults appeared in the field from midspring (October, when *X. s. cavanillesii* plants were about 30–40 days old) to midsummer, with the greatest density occurring at the beginning of December (Fig. 1). The presence of eggs in the field coincided with this period. Females laid eggs individually inside the stems and the larvae bored the stems toward the root. In the fall, when plants became dry, the larvae girdled the stems, about 3 cm above the crown, causing the aerial part of the plant to fall over. The larval period in the field lasted 9–12 months, including diapause (Fig. 1). Larval development lasted 105–135 days, before last instar entered diapause. The last instar entered diapause in the stump and pupated there during the following spring (Fig. 1). Pupae were found from the beginning of October to the end of December. Peak populations occurred during the second half of November (Fig. 1). During 1987–88 and 1988–89, 22.9% and 59.0% of *X. s. cavanillesii* plants, respectively had either mature larvae or had the main stem bored by *A. versicolor*.

3.1.1. Adults

Adults had an average length of 8.37 ± 1.05 mm ($n = 54$). They were diurnal and mostly active between 10:00 a.m. and 4 p.m. Adults did little damage to host plants; they fed on veins and superficial adjacent tissues of the undersides of the leaves. Adults of both sexes stridulated if disturbed. In the laboratory, the average longevity was 18.5 days (range 8–44, $n = 36$). Difference in longevity between males and females was not significant ($t = -1.31$; $df = 34$; $P = 0.19$). Females laid an average of 38 eggs each (range 12–116), 66% of which was oviposited during the first week (Fig. 2).

Females oviposited in the stems around the axils of petioles and secondary branches. At the selected site, they broke the outer tissue of the plant with their mandibles and then made a puncture with their ovipositor in the wound. The search for the oviposition site took 1–5 min and oviposition took 2–3 min. When the ovipositor was withdrawn, a small rounded scar (about 1 mm diameter) was observed on the stem surface. However, some females made the puncture with their ovipositor but did not deposit an egg. Although this behavior was not quantified, it was frequent enough to conclude that oviposition marks should not be used to estimate the number of eggs.

3.1.2. Eggs

Eggs were inserted 2–3 mm deep, parallel to the stem surface. When turgid, eggs were 1.31 ± 0.1 mm long and 0.48 ± 0.03 mm wide. Most were generally ovoid ($n = 39$), but some were cylindrical ($n = 11$). The mean incubation period was 10 days (range 9–11). Viability was estimated at 88%.

3.1.3. Larvae

In the laboratory, larvae had seven instars. The width of the gula appeared as a good indicator of instars since measured widths were not much different from expected values calculated using Dyar's ratio (Table 1). When the larva was ready to hatch from the egg, it made a series of longitudinal contraction-stretching movements that made the spines on the mandibles tear the chorion apically, producing an orifice through which the larva emerged. After hatching, the larvae started to feed in any direction, but after a few days they bored the stems toward the roots. In the field, multiple larvae in single-stemmed plants of *X. s. cavanillesii* showed a marked competitive exclusion due to cannibalism. This process triggered when two larvae met and was observed in both young and mature larvae. Toward the end of fall, the last instar larvae chewed an inner circular girdle at the base of the stem. Therefore, wind or a passing animal could then break off the dry stem, leaving a stump (which included the root and a small basal part of the stem). Inside the stump, the larva was protected from the outside by a plug of chewed wood fibers. By the time the plants fell over due to the larval girdling, the plants were dead and the burs were mature. The average height of the girdled cut was 3.5 ± 1.5 cm ($n = 114$ plants) above the ground level. Inside the stump, the larva entered diapause.

Table 1
Comparison of observed (mode) and expected values of Gula widths (mm) of larvae of *A. versicolor*

Instar	Mode	Range	Expected[a]	Difference (%)
I	0.22	0.20–0.24	0.22	0.0
II	0.28	0.26–0.30	0.28	0.0
III	0.33	0.30–0.37	0.35	+6.1
IV	0.45	0.39–0.54	0.45	0.0
V	0.59	0.52–0.63	0.57	−3.4
VI	0.72	0.62–0.76	0.73	+2.8
VII	0.87	0.75–1.0	0.92	+6.1

[a] Calculated from the mean of observed Dyar ratios ($r = 1.27$).

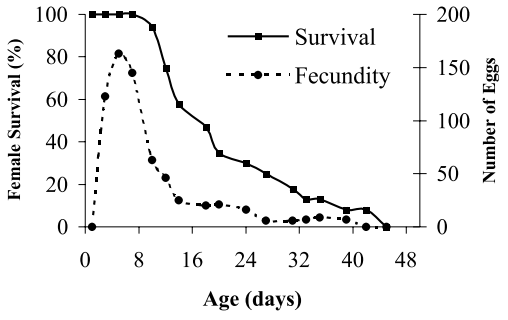

Fig. 2. Age-specific fecundity and survival of female *A. versicolor*. Survival is expressed in percentages, and fecundity is expressed by total number of eggs for each percentage of female survival.

The girdling behavior of the last instar may have an adaptive value. The stump may provide larvae with shelter from weather conditions and to escape from predation. Girdling and the fiber plug may decrease colonization by additional larvae and thus prevent intraspecific competition for pupation space and cannibalism. It may also decrease the availability of the pupa to predators (e.g., ants). Prior to pupation, the larva became rigid and made circular twisting movements around its longer axis. In the laboratory, *A. versicolor* reduced 66% of the seed production when it attacked 45-day-old plants of *X. s. cavanillesii*. However, fruit reduction decreased to 23% in 75 days-old attacked plants (Gandolfo et al., 1997).

3.1.4. Pupae

Pupation occurred in the stumps. The pupal stage lasted 23.1 ± 2.2 at 20 °C, 13.3 ± 2.0 at 25 °C, and 8.7 ± 1.1 at 30 °C. The lower threshold for pupal development was 11.7 °C, the constant K for the pupa was 154 degree-days. The regression line used to estimate the development threshold temperature is given in Fig. 3.

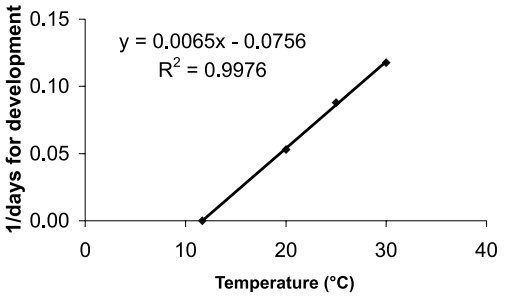

Fig. 3. Temperature requirement for *A. versicolor* to complete the pupal stage; lower threshold for development = 11.7 °C ($K = 154$ degree-days).

3.2. Resistance of overwintering larvae to cold and immersion

All larvae were alive after 13 days at 4 and 0 °C. Six (75%) larvae were alive after 13 days at −4 °C. The survival rate decreased at −8 °C with increasing exposure time from 100% at 1 day, to 88% at 3 days, and 37.5% after 13 days. Two larvae (25%) lived 1 day at −14 °C, and none survived after 3 days or more at this temperature (Table 2).

Overwintering larvae survived for at least 20 days when submerged under water regardless of whether they were removed from the stumps and placed in glass vials, or retained in the girdled stumps (Table 3). No difference between the results of the two tests was detected. Thus, we conclude that larvae are adapted to survive immersion. In spite of the ability of the larvae to survive immersion, long-lasting floods are an important abiotic factor of mortality. During 1988 and 1989, when floods occurred at the beginning of the summer, the plants close to shore died and consequently the young larvae died of starvation.

3.2.1. Diapause

Results were incomplete because out of the 259 initial larvae in the test, less than 10% reached the pupal stage. A pathogen infected more than 60% of the larvae and the parasitoid *Nealiolus* sp. emerged from 30% of the larvae. Nevertheless, results showed that larvae exposed to temperatures between 0 and 12 °C for at least 4 days and then exposed to 30 °C pupated in 5.3 ± 1.4 weeks ($n = 13$). The larvae used as controls and those exposed to low temperatures for 1–2 days took a significantly longer time ($F = 27.73$; df $= 1, 18$; $P < 0.05$) to reach the pupal stage, 8.3 ± 0.8 weeks ($n = 7$).

Table 2
Survival of overwintering larvae of *A. versicolor* at five temperatures[a]

Exposure (days)	Larvae (%) that survived at each temperature				
	+4 °C	0 °C	−4 °C	−8 °C	−14 °C
1	100.0	100.0	100.0	100.0	25.0
3	100.0	100.0	100.0	87.5	0.0
7	100.0	87.5	100.0	50.0	0.0
10	100.0	100.0	87.5	62.5	–
13	100.0	100.0	75.0	37.5	–

[a] Eight larvae tested for each treatment.

Table 3
Survival of overwintering larvae of *A. versicolor* under six submersion regimes[a]

Submergence (days)	No. of surviving larvae	
	Inside roots	In glass vial
3	9	10
5	10	10
7	9	10
10	9	8
15	10	10
20	10	10

[a] Ten larvae tested in each treatment.

3.3. Geographic distribution

In Argentina, *A. versicolor* was found from the north of the country, Salta Province, (22°S) down to Rio Negro Province (40°S) (Fig. 4). *A. versicolor* was collected from all the main phytogeographical regions: Yungas (subtropical rain forest), Chaco (forest), Monte (desert), and Espinal (ecotone between forest and desert), except from the Patagonian plateau.

3.4. Seasonal occurrence of parasitoids in Buenos Aires

In the collecting site near Hurlingham where the field studies were carried out, the larvae of *A. versicolor* were found parasitized by *Nealiolus* n. sp. (Hymenoptera: Braconidae), *Agonocryptus* sp. (Hymenoptera: Ichneumonidae), and *Bracon* sp. (Hymenoptera: Braconidae).

Between October 1987 and January 1988, 40 (18%) larvae of *A. versicolor* were parasitized by *Nealiolus* n. sp., and in 1988–89, 162 (61.5%) larvae were parasitized (Table 4). Parasitism by *Bracon* sp. and *Agonocryptus* sp. was less than 5% during the two seasons in which samples were taken (Table 4). Adults of *Bracon* sp. emerged from mid-March to early April, when plants of *X. s. cavanillesii* started to dry. Adults of *Agonocryptus* sp. emerged from mid-November to late December. *Agonocryptus* sp. emerged only from larvae collected in spring, not from larvae sampled during fall and winter.

Studies conducted in the laboratory showed that *Nealiolus* n. sp. left its host as a larva and pupated a few days later (5.0 ± 2.2; $n = 10$) in a cocoon inside the roots. The adult took 15 days ($n = 36$), range 11–21 days, to emerge at 30 °C. The larvae of *A. versicolor* were parasitized in early instars, but the parasitoid larvae emerged from overwintering larvae of *A. versicolor*. Parasitoids of pupae and adults of *A. versicolor* were not found.

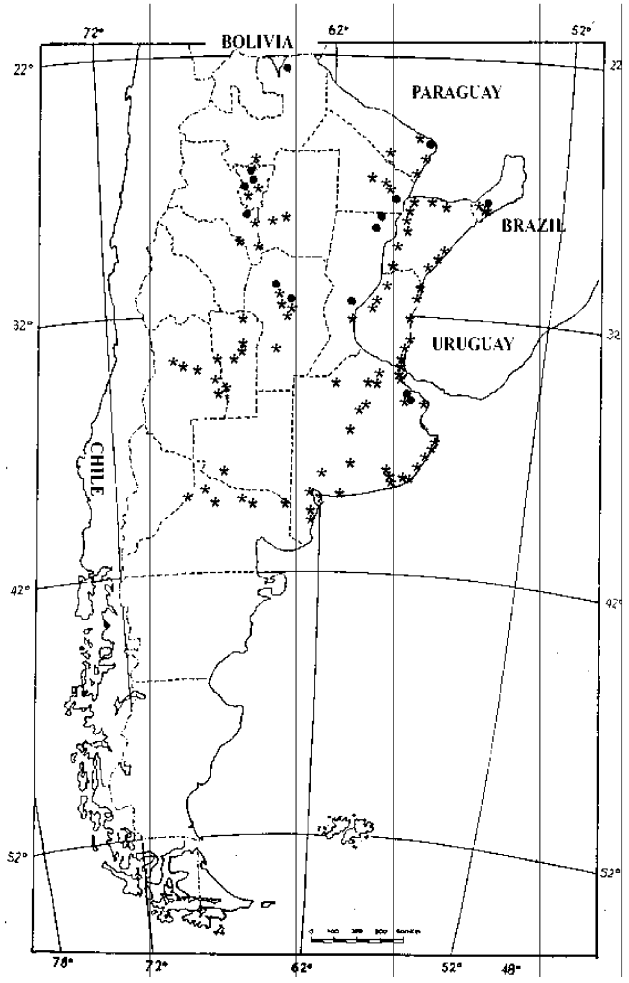

Fig. 4. Distribution of *A. versicolor* in Argentina, data from field collections (*) and museum records (•).

Table 4
Occurrence and abundance of parasitoids of *A. versicolor* in Buenos Aires, Argentina

Parasitoids	Parasitoids emerged *n* (%)	
	1987/88[a]	1988/89[b]
Nealiolus sp.	40 (18)	162 (61.5)
Agonocryptus sp.	5 (2)	12 (4.5)
Bracon sp.	0 (0)	11 (4.2)

[a] In 1987–88, 23% of 1000 randomly selected plants of *X. s. cavanillesii* were infested with *A. versicolor*; 213 larvae were examined for parasitoids.

[b] In 1988–89, 59% of 1800 randomly selected plants of *X. s. cavanillesii* were infested with *A. versicolor*; 264 larvae were examined for parasitoids.

4. Conclusion

We conclude that *A. versicolor* has several biological attributes that suggest that it could be an effective biological control agent for *Xanthium* spp.: (1) 45-day-old plants infested by *A. versicolor* reduced fruit production by 66%; attack of younger plants caused the plants to die (Gandolfo et al., 1997); (2) the insect is cold and immersion tolerant; (3) it has a wide phytogeographical distribution, from tropical forest to desert, and (4) has diapause, which is important since the host is an annual weed that dries up in winter.

Acknowledgments

The authors thank Luis De Santis (Universidad Nacional de La Plata) for identifying the parasitoids of *A. versicolor* and Angel Cabrera (Instituto Darwinion), for identifying *Xanthium* spp. They also thank Martín Carranza for assisting with the laboratory and field experiments; C. Jack DeLoach (Temple, TX, USDA-ARS) and Karen Braun, who provided advice in the preparation of the manuscript, and Arabella Bugliani, who improved the readability of the manuscript.

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